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AFLP analysis of genetic diversity within a jackfruit germplasm collection

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Abstract

Twenty-six jackfruit accessions, one interspecific hybrid, champedak, and one breadfruit accession were analyzed using amplified fragment length polymorphic (AFLP) markers to determine the degree of genetic diversity within the Fairchild Tropical Garden (FTG) germplasm collection. Of the 30 primer pairs evaluated, 12 were identified for collection screening based on number and quality of polymorphic fragments. A total of 187 AFLP markers were scored using the 12 primer pairs, 92 (49.2%) being polymorphic. All accessions could be uniquely identified using the 12 primer pairs. Among the jackfruit accessions, similarity coefficients ranged from 0.567 to 0.950; the accessions also shared a large number of monomorphic fragments (54.9%). Cluster analysis and principal component analysis (PCA) grouped all of the jackfruit accessions with south-east Asian origins into one major cluster with little bootstrap support for groupings within the cluster. The Indian accessions were grouped in a different cluster, as did the hybrid and the breadfruit accession. The AFLP marker based analysis indicates that limited genetic diversity exists within this collection. These observations are in agreement with the phenotypic evaluation and suggest that new accessions be obtained from the center of origin for the species. Published by Elsevier Science B.V.

Keywords: *Artocarpus*; Jackfruit; Genetic diversity; AFLP; PCR; Molecular markers

1. Introduction

The jackfruit (*Artocarpus heterophyllus* Lam., Moraceae) is believed to have originated in the Western Ghats region of India. It has been cultivated for

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centuries in the lowland rainforests of south-east Asia where it is widely grown commercially and in the home garden (Acedo, 1992; Samaddar, 1985; Soepadmo, 1991). Superior selections have been propagated vegetatively in these regions, many maintained until the present day. The highly versatile fruit is used green as a cooked vegetable, eaten fresh when ripe, and included in many regional cuisines. The large, starchy seeds can be cooked and eaten, and the fibrous rind of the fruit fed to livestock. In the western hemisphere, the jackfruit is much less known or appreciated, although it was introduced to many countries over a century ago. With the exception of Brazil and parts of the West Indies, it has remained a tropical fruit of minor importance (Fairchild, 1946). The large size of the fruit, unusual appearance, and strong aromas contribute to the jackfruit's slow acceptance in American markets.

Jackfruit is gaining popularity in the United States due to the availability of superior germplasm, modern growing techniques, and emerging ethnic and mainstream marketing opportunities (Campbell and El-Sawa, 1998; Campbell et al., 1998). A small collection of jackfruit cultivars has been established at FTG which is providing germplasm throughout tropical America (Campbell and McNaughton, 1994). A few varieties have been selected for production in south Florida and have contributed to a substantial increase in the commercial production. In order to enhance the development of this crop, there is a need for a greater understanding of the genetic diversity that is present among the clonal material in this collection and among jackfruit germplasm throughout the region.

Amplified fragment length polymorphism (AFLP) markers are a recently developed system that combines the specificity of restriction enzyme analysis with the relative technical simplicity of the polymerase chain reaction (PCR) (Vos et al., 1995). AFLPs have been used to fingerprint accessions, for genetic linkage mapping, and for genetic diversity analysis. They have the advantages that they are easy to use, sample a large number of loci per reaction, and are reproducible between laboratories. They do have the same disadvantage as randomly amplified polymorphic DNA markers that they are inherited in a dominant manner.

A genetic improvement program has been initiated at FTG in collaboration with the USDA National Germplasm Repository (NGR, Miami) with the goal of producing improved jackfruit cultivars for commercial production and home gardens. To initiate the improvement effort, a basic understanding of the genetic relationships among the clones was considered essential. We report here on the results of a genetic diversity analysis of the jackfruit accessions based on AFLP analysis. Our goals were to try to differentiate the named clones of jackfruit and to understand the genetic relationships among clones in the collection.

2. Materials and methods

2.1. Plant material

In this study, 26 accessions of jackfruit, one interspecific hybrid (*A. heterophyllus* × *A. integer* Merr.) and one breadfruit (*A. altilis* Fosberg) accession were collected from the germplasm collection at FTG. Tissue samples were weighed out to 50 mg and stored at −80°C (Table 1).

2.2. DNA extraction

DNA extraction was performed with the Dellaporta method scaled down for microcentrifuge use (Schnell et al., 1996) with the following modifications for

Table 1
List of origins of *Artocarpus* used in AFLP analysis

Cultivar	Species	Accession #	Origin
Bali Beauty	*A. heterophylus*	94-1326 A	Indonesia
Black Gold	*A. heterophylus*	87-678 B; 87-678 C	Australia
Bogor Big	*A. heterophylus*	94-1325	Indonesia
Cheena	*A. heterophylus* × *A. integer*	89-758 A; 89-758 B	Australia
Cochin	*A. heterophylus*	94-355 A	Australia
Chompa Gob	*A. heterophylus*	96-1488 A; 96-1488 B	Thailand
Dang Rasimi	*A. heterophylus*	89-697 B; 89-697 C	Thailand
Galaxy	*A. heterophylus*	89-756 A; 89-756 B	Australia
Giant Jack	*A. heterophylus*	94-259 A	Indonesia
Golden Nugget	*A. heterophylus*	87-679 A; 87-679 C	Australia
Honey Gold	*A. heterophylus*	88-292 A; 88-292 B	Australia
J31	*A. heterophylus*	87-605 A; 87-605 B	Malaysia
Lemon Gold	*A. heterophylus*	88-291 A	Australia
Long John	*A. heterophylus*	94-542 A	India
Lueng Bang	*A. heterophylus*	93-881 A	Thailand
Manatee	*A. heterophylus*	88-351 A	Cambodia
NS1	*A. heterophylus*	88-682 A	Malaysia
Pani Varaka	*A. heterophylus*	94-543 A	India
J30	*A. heterophylus*	88-350 B	Malaysia
Seedling a	*A. heterophylus*	95-45 A	Florida
Seedling b	*A. heterophylus*	95-45 B	Florida
Seedling d	*A. heterophylus*	95-45 D	Florida
Singapore	*A. heterophylus*	95-1537	Singapore
Tabouey	*A. heterophylus*	87-494 B; 87-494 C	Indonesia
TREC #1	*A. heterophylus*	93-882 A	Thailand
TREC #2	*A. heterophylus*	95-46 A	Thailand
Whitman	*A. heterophylus*	95-47 A	Florida
Breadfruit	*A. altilis*	MIA 35550	Florida

leaf tissue. Fifty milligram of frozen leaf samples were ground with liquid nitrogen followed by the addition of 500 μl of extraction buffer. The supernatant removed after the first centrifugation was transferred to a clean tube and centrifuged for the second time at 16,000 g for 10 min, followed by ethanol precipitation. After drying, the DNA was resuspended in 30 μl TE, pH 7.4. DNA concentration was determined by use of a DynaQuant 200 fluorometer (Hoefer Pharmacia, San Francisco, CA). Duplicate extractions were performed for each accession.

2.3. AFLP procedure

The AFLP technique was accomplished with fluorescent dye-labeling and detection technology. Fluorescent detection was performed on an automated capillary electrophoresis apparatus, the ABI Prism 310 Genetic Analyzer (PE Applied Biosystems, Foster City, CA). The AFLP™ plant mapping kit was purchased from Applied Biosystems and the protocol carried out according to manufacturers' directions (PE Applied Biosystems, 1996). Polymerase chain reactions (PCRs) were performed on a PTC-100 thermal cycler (MJ Research, Watertown, MA) or on an ABI Prism 877 integrated thermal cycler (Applied Biosystems).

Initially, the quality of the genomic DNA was tested by evaluating restriction digests. Five hundred nanograms of genomic DNA was used in the restriction-ligation of *Eco*RI and *Mse*I adapters. Pre-selective amplification was performed on diluted restriction-ligation reaction products with pre-selective primers. Pre-selective amplification primers have the cut site adapter sequence plus one additional nucleotide extension at the 3′ end. The *Eco*RI complimentary primer has a 3′ A, while the *Mse*I complimentary primer has a 3′ C. Pre-selective amplification cycle profile was as follows: 72°C incubation for 2 min, then cycled 20 times (denaturation 94°C for 1 s, annealing 56°C for 30 s, extension 72°C for 1 min). Selective amplification was performed on diluted pre-selective amplification products with the following cycling profile: one cycle of 94°C for 2 min, 65°C for 30 s, 72°C for 2 min; followed by 9 cycles with annealing temperatures decreasing by 1°C each cycle starting with 94°C for 1 s, 64°C for 30 s, 72°C for 2 min; and ending with 23 cycles of 94°C for 1 s, 56°C for 30 s, 72°C for 2 min. The selective amplification primer pairs have an additional three nucleotide extension at the 3′ end (Table 2). In all reactions only the *Eco*RI primers were 5′ labeled with a fluorescent dye (Applied Biosystems). Primer selection was performed on several sub-sets of the samples using 30 different primer pair combinations. Based on the results obtained, such as peak resolution and average band numbers, 12 primer pairs were selected (Table 2) and selective amplification was carried out on all samples. Single PCRs were performed for each primer combination and the products from three primer pairs (with different dyes) were

Table 2
Selected primers and level of polymorphism among *Artocarpus* accessions from AFLP analysis

Selective amplification primer pairs	Number of polymorphic peaks for *A. heterophyllus*	Number of polymorphic peaks for *Artocarpus spp.*	Total number of peaks for *A. heterophyllus*	Total number of peaks for *Artocarpus spp.*
*Eco*RI-ACA FAM + *Mse*I-CAC	5	7	15	17
*Eco*RI-ACA FAM + *Mse*I-CTA	9	11	14	16
EcoRI-ACT FAM + *MseI*-CAA	5	6	13	14
*Eco*RI-ACT FAM + *Mse*I-CAC	14	17	24	27
*Eco*RI-AAC NED + *Mse*I-CAC	9	10	14	15
*Eco*RI-ACC NED + *Mse*I-CAA	4	4	12	12
*Eco*RI-ACC NED + *Mse*I-CAC	13	15	25	27
*Eco*RI-ACC NED + *Mse*I-CTG	7	7	18	18
*Eco*RI-ACG JOE + *Mse*I-CTA	2	3	3	4
*Eco*RI-AGG JOE + *Mse*I-CAC	3	4	9	10
*Eco*RI-AGG JOE + *Mse*I-CAG	6	6	15	15
*Eco*RI-AGG JOE + *Mse*I-CTG	1	2	11	12
Total	78	92	173	187

multiplexed for electrophoresis. Samples were prepared immediately before electrophoresis by combining 1 μl of each of the three selective amplification products, 12 μl of deionized formamide and 0.5 μl of GeneScan-500 ROX-labeled internal lane size standard (Applied Biosystems), denaturing for 2 min at 94°C and chilling on ice. Capillary electrophoresis was carried out on two ABI PRISM 310 genetic analyzers using POP 4 capillary polymer and ABI Prism 310 electrophoresis buffer (Applied Biosystems). The capillaries were 47 cm in length with 50 μm ID. Samples were injected electrokinetically for 5–20 s at 15 kV and electrophoresed at 15 kV for 24 min at 60°C. Data were collected using GeneScan software (version 2.1, Applied Biosystems). The threshold value for peak detection varied per primer pair, ranging between 25 and 40 fluorescent units.

2.4. Data analysis

Combined data files containing data for all samples were created using GeneScan analysis software and further analyzed using Genotyper software (version 1.2, Applied Biosystems) for each primer combination. Amplification products were scored for presence (1) or absence (0) of peaks. Peaks common to all accessions were considered as non-informative. A pairwise similarity matrix between genotypes was estimated according to Nei and Li (1979). The similarity coefficient

$$S_{ij} = \frac{2a}{(2a + b + c)}$$

where S_{ij} is the similarity between two individuals i and j, a the number of positive peaks shared by both individuals, b the number of peaks present in i and absent in j and c the number of peaks present in j and absent in i. The SAHN clustering program was then used to group the entries based on similarity coefficients using the unweighted pair-group method using arithmetic average (UPGMA) using NTSYS (Exeter Software, Setauket, NY). A phenetic tree was constructed and confidence limits placed on the dendrogram using the bootstrapping program WinBoot with 5000 bootstrap replications (Yap and Nelson, 1996). Principal component analysis (PCA) of the correlation matrix was used to further investigate relationships between individuals using SAS Version 7.0 (SAS Institute, Cary, NC).

3. Results and discussion

The accessions evaluated in this study include seven from Australia, four from Indonesia, five from Thailand, three from Malaysia, two from India, one each

from Cambodia and Singapore, and five from Florida (Table 1). Also analyzed was a single interspecific hybrid between *A. heterophyllus* × *A. integer*, known as champedak, and a single accession of breadfruit. Replicate accessions (Table 1) represent individual trees clonally propagated from the original source tree. Unfortunately the origin of most of these accessions cannot be more precisely identified as many of the FTG database records contain only source information. Jackfruit has been under cultivation in south-east Asia for centuries and the true origin of material may not be at all related to the source from which it was obtained. This information is often based solely on the recollections of those from whom the material was received. It is likely that the accessions listed from Florida and Australia originated in south-east Asia. Under south Florida conditions, the accessions differ in tree vigor, fruit production, size, shape, exterior color, flesh texture, flesh color, aroma, percent edible flesh, seed weight and number, season, growth rate, and canopy growth habit (Campbell and El-Sawa, 1998).

The Applied Biosystems AFLP kit contains eight *Eco*RI and eight *Mse*I primers for a total of 64 combinations available for amplification reactions. Initially several subsets of five jackfruit accessions were used to determine the combination of primers to be used. Thirty primer combinations were screened and 12 were selected for the analysis. The 18 primer sets tested but not selected contained primarily monomorphic peaks, poorly resolved peaks, or yielded no amplification products. The overall reproducibility of the AFLP amplification patterns among the 12 selected primer pairs was good. Approximately 1% of the amplifications from replicate DNA isolations, from the same accession, produced pattern differences. Only peaks that were reproducible across extractions were scored and used for the analysis. Amplification products resulting from using primers *Eco*RI-ACA FAM and *Mse*I-CAC are illustrated in Fig. 1. Duplicated amplification reactions for three accessions showing peaks at 138, 140, 146, and 148 base pairs for 'Black Gold', 'Cochin', and 'NS1' give reproducible results. The polymorphic 146 base pair peak is present in 'Black Gold' and 'Cochin' but absent in 'NS1'.

A total of 187 peaks were scored with sizes ranging from 50 to 396 bp from the 12 primer pair combinations selected for the analysis. Each individual accession was uniquely identified with the 12 primer pair combinations. Of the 187 peaks scored, 92 (49.2%) were polymorphic. The number of polymorphic peaks per primer combination ranged from 2 to 17 with the average number of polymorphic peaks being 7.6 (Table 2). Only 92 polymorphic peaks were used for the phylogenetic analysis. Of these, 78 were polymorphic for jackfruit, yielding 45.1% polymorphism for jackfruit alone. This level of polymorphism is higher than reported for many intraspecific AFLP studies, 11.8% in wheat cultivars adapted to the north-west Pacific (Barrett and Kidwell, 1998) and 10% among celery cultivars grown in California (Li and Quiros, 2000). However, high levels

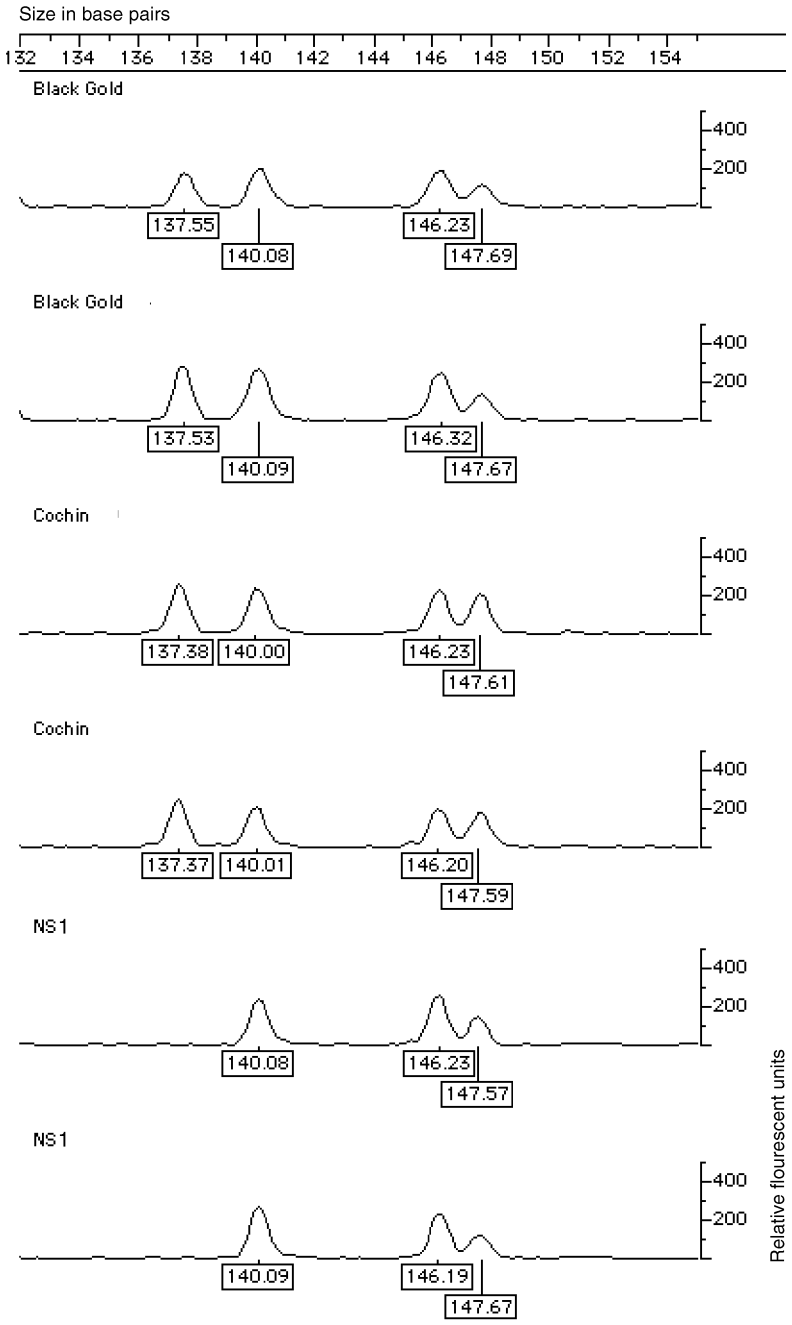

Fig. 1. AFLP profiles of three accessions with two replications produced from primer pair *Eco*RI-ACA FAM and *Mse*I-CAC.

of polymorphism (90%) have been found in other studies where wild gene pools were evaluated (Tohme et al., 1996). Li and Quiros (2000) attributed the low level of polymorphism in celery to a large genome size with extensive areas of repetitive DNA. The genome size of *Artocarpus* is unknown. The basic chromosome number for the genus is $x = 14$ and for *A. heterophyllus* is $2n = 56$ (Darlington and Wylie, 1945).

The genetic similarity coefficients based on the fluorescent-labeled AFLP data between *A. altillis* and the jackfruit cultivars ranged from 0.175 to 0.333 (Table 3). The genetic similarity coefficients between the champedak and the jackfruit accessions ranged from 0.441 to 0.642. Using RFLPs of cpDNA from a number of *Artocarpus* spp., Kanzaki et al. (1997) reported that *A. heterophyllus* and *A. integer* could not be distinguished and that *A. altilis* clustered closely with *A. elasticus* but was distinguishable from *A. heterophyllus*. The low genetic similarity coefficients between the breadfruit accession and jackfruit accessions and the higher values for the chempedak and jackfruit accessions are in agreement with their observations. Among the jackfruit accessions, genetic similarity coefficients ranged from a low of 0.567 to a high of 0.950 with a high average similarity among this group of accessions of 0.743 (Table 3). Kanzaki et al. (1997) found that they could not distinguish jackfruit and chempedak using cpDNA and RFLP markers. In the present study, the single interspecific hybrid accession, 'Cheena', was easily distinguished using the AFLP markers. The large number of consistent, non-variable markers found among the 12 selected primer pairs (50.8%) and the large number found among the primer pairs not used in this study (78.2%) further support the finding of limited levels of genetic diversity within this collection.

The UPGMA tree generated by the similarity coefficients grouped 24 of the jackfruit accessions into one major cluster labeled Cluster I. The two Indian accessions grouped in another cluster labeled Cluster II. 'Cheena' and *A. altilis* were separated from the jackfruit accessions. The bootstrap value was high (76.3%) for the clustering of accessions 'NS1' and 'Seedling a', 'Seedling b', and 'Seedling d'. This clustering is expected as these are maternal half-sibs of 'NS1'. 'Honey Gold', 'Lemon Gold' and 'J30' also cluster with a high bootstrap value, as do 'Tabouey' and 'TREC #1'. The two Indian cultivars, 'Long John' and 'Pani Varaka', also cluster together with high bootstrap values and are distant from other jackfruit accessions. These results are interesting as India has been reported as the possible origin for cultivated jackfruit, and therefore presumably the center of diversity for jackfruit (Soepadmo, 1991). All other clusters were not well supported by the bootstrap values (Fig. 2).

The PCA also supports the aforementioned grouping as illustrated in Fig. 3. PCA was able to summarize 37.9% of the total variability onto the three axes shown in this plot (17.8, 11.2, and 8.9%, respectively, for Prin1, Prin2, and Prin3). PCA without 'Cheena' and breadfruit is illustrated in Fig. 4, containing

Table 3
Similarity coefficients among 28 *Artocarpus* accessions

	Cultivar	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1	Bali Beauty	1.000																											
2	Black Gold	0.764	1.000																										
3	Bogor Big	0.767	0.774	1.000																									
4	Cheena	0.611	0.565	0.606	1.000																								
5	Cochin	0.648	0.666	0.641	0.441	1.000																							
6	Chompa Gob	0.744	0.709	0.711	0.516	0.692	1.000																						
7	Dang Rasimi	0.759	0.767	0.722	0.512	0.647	0.674	1.000																					
8	Galaxy	0.794	0.705	0.731	0.617	0.657	0.707	0.666	1.000																				
9	Giant Jack	0.781	0.744	0.747	0.577	0.708	0.835	0.738	0.795	1.000																			
10	Golden Nugget	0.717	0.776	0.682	0.518	0.657	0.682	0.720	0.567	0.698	1.000																		
11	Honey Gold	0.780	0.741	0.767	0.611	0.675	0.744	0.708	0.769	0.781	0.717	1.000																	
12	J31	0.814	0.704	0.776	0.642	0.630	0.776	0.717	0.805	0.837	0.649	0.839	1.000																
13	Lemon Gold	0.767	0.774	0.822	0.561	0.743	0.755	0.746	0.756	0.835	0.756	0.860	0.800	1.000															
14	Long John	0.693	0.658	0.658	0.538	0.626	0.683	0.694	0.676	0.725	0.676	0.613	0.675	0.658	1.000														
15	Lueng Bang	0.729	0.717	0.741	0.477	0.597	0.696	0.756	0.641	0.711	0.666	0.705	0.761	0.808	0.666	1.000													
16	Manatee	0.750	0.712	0.761	0.578	0.694	0.785	0.779	0.657	0.800	0.763	0.775	0.784	0.809	0.712	0.746	1.000												
17	NS1	0.765	0.727	0.729	0.571	0.712	0.776	0.743	0.805	0.813	0.753	0.765	0.850	0.823	0.702	0.738	0.810	1.000											
18	Pani Varaka	0.626	0.622	0.620	0.441	0.586	0.643	0.675	0.582	0.636	0.632	0.578	0.609	0.643	0.815	0.651	0.666	0.658	1.000										
19	J30	0.771	0.755	0.781	0.581	0.720	0.758	0.750	0.759	0.795	0.734	0.891	0.853	0.919	0.657	0.767	0.814	0.853	0.642	1.000									
20	Seedling a	0.756	0.764	0.767	0.588	0.702	0.767	0.784	0.769	0.804	0.743	0.780	0.839	0.813	0.693	0.752	0.825	0.913	0.674	0.867	1.000								
21	Seedling b	0.814	0.772	0.752	0.595	0.712	0.800	0.794	0.779	0.813	0.779	0.765	0.825	0.800	0.729	0.738	0.835	0.925	0.682	0.829	0.913	1.000							
22	Seedling d	0.750	0.758	0.761	0.578	0.722	0.761	0.779	0.736	0.800	0.763	0.775	0.810	0.809	0.684	0.746	0.820	0.911	0.641	0.839	0.950	0.936	1.000						
23	Singapore	0.800	0.758	0.785	0.602	0.722	0.833	0.753	0.789	0.823	0.710	0.825	0.835	0.809	0.684	0.746	0.846	0.835	0.617	0.839	0.825	0.886	0.846	1.000					
24	Tabouey	0.810	0.744	0.795	0.609	0.704	0.795	0.815	0.746	0.809	0.693	0.759	0.820	0.746	0.666	0.707	0.831	0.769	0.600	0.775	0.810	0.846	0.805	0.857	1.000				
25	TREC #1	0.819	0.755	0.804	0.581	0.666	0.758	0.825	0.734	0.818	0.734	0.746	0.780	0.804	0.657	0.767	0.864	0.780	0.595	0.761	0.795	0.804	0.790	0.790	0.900	1.000			
26	TREC #2	0.658	0.764	0.674	0.541	0.621	0.720	0.683	0.666	0.804	0.717	0.682	0.716	0.720	0.693	0.682	0.750	0.716	0.626	0.698	0.731	0.765	0.725	0.750	0.734	0.722	1.000		
27	Whitman	0.813	0.817	0.822	0.561	0.743	0.800	0.795	0.780	0.813	0.756	0.813	0.776	0.822	0.734	0.764	0.809	0.776	0.712	0.804	0.790	0.800	0.785	0.833	0.771	0.804	0.744	1.000	
28	*A. altilis*	0.333	0.262	0.310	0.385	0.217	0.241	0.196	0.320	0.305	0.280	0.296	0.301	0.275	0.212	0.175	0.307	0.264	0.181	0.254	0.296	0.264	0.269	0.230	0.313	0.327	0.222	0.241	1.000

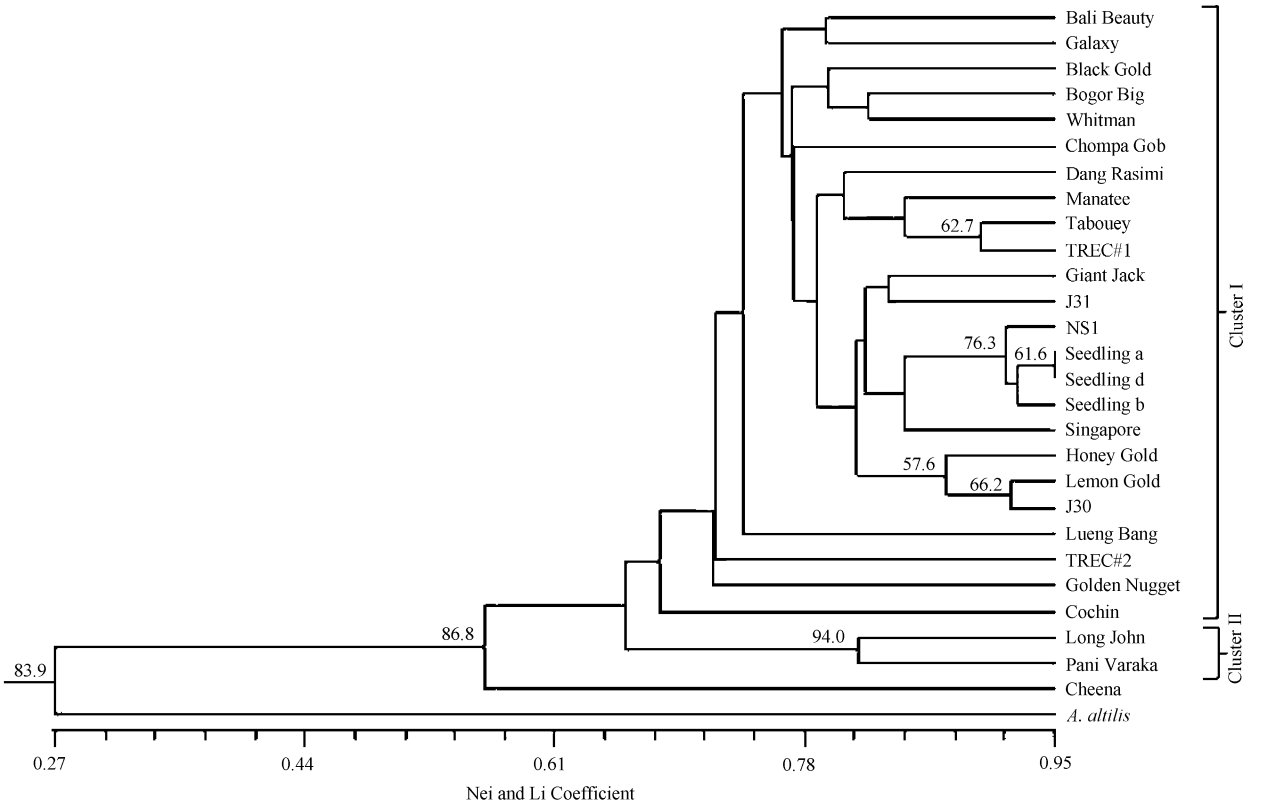

Fig. 2. UPGMA-based dendrogram of jackfruit and breadfruit accessions generated from 92 AFLP markers. The numerical scale indicates increasing genetic similarity. Confidence limits for the dendrogram are based on 5000 bootstrap replications. Only bootstrap values greater than 50% are reported.

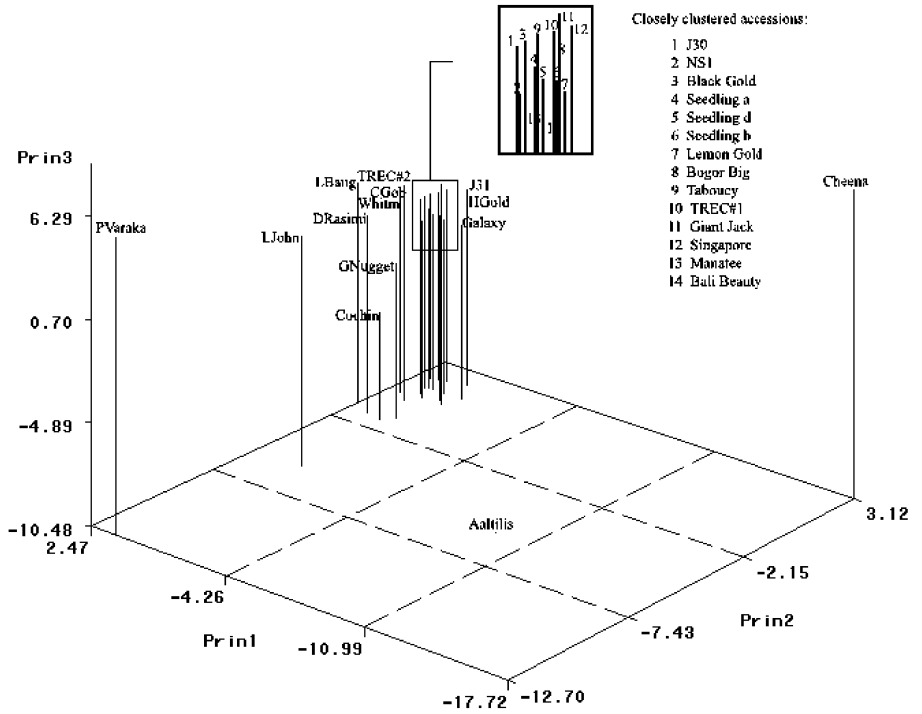

Fig. 3. Principal components analysis for 26 jackfruit accessions, one chempadak and one breadfruit accession based on 92 AFLP markers. This plot contains 37.9% of the total variability, 17.8% on the first principal component axis, 11.2% on the second, and 8.9% on the third.

30.8% of the total variability, where associations can be seen among clusters which had high bootstrap values in the cluster analysis such as 'NS1' and 'Seedling a', 'Seedling b', and 'Seedling d'. Principal coordinates analysis of the distance matrix (not shown) produced graphs resulting in the same conclusions.

Preliminary phenotypic evaluation of the jackfruit accessions analyzed in this study indicated that for many traits the accessions are very similar. Differences among accessions do occur; however, these estimates are confounded by the non-standardization of rootstocks, the evaluation in a single environment, and the effects of genotype × environment interaction. The phenotypic data tend to support the molecular analysis and indicate that a more extensive collection effort for jackfruit germplasm will be required to broaden the genetic base for the breeding program. The acquisition of new accessions should be concentrated in India, as a center of diversity for the species. Currently, only two accessions in the collection are from India and these are different from the south-east Asian accessions.

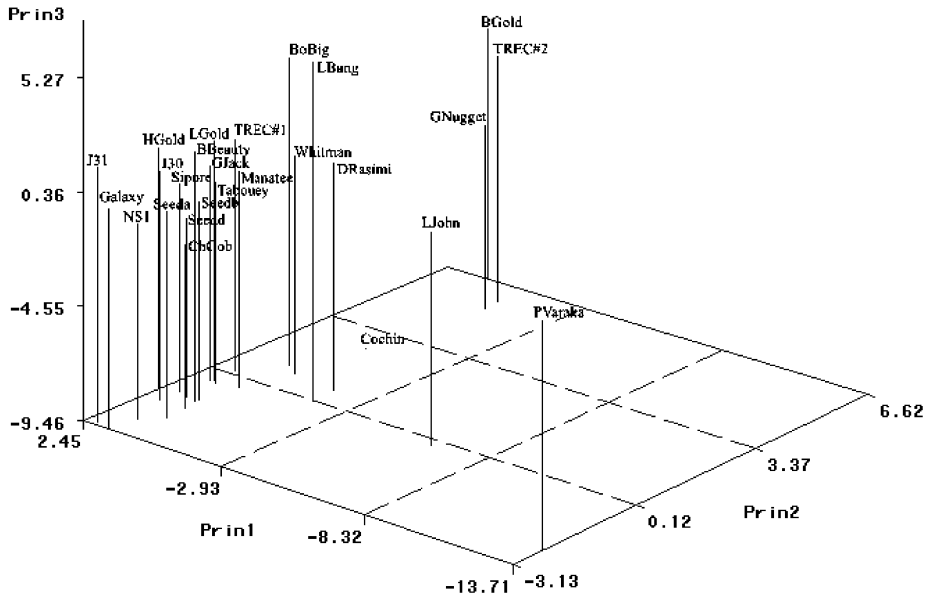

Fig. 4. Principal components analysis for 26 jackfruit accessions based on 78 AFLP markers. This plot contains 30.8% of the total variability, 14.1% for the first principal component axis, 8.4% for the second, and 8.3% for the third.

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